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A REVIEW OF THE INVERTEBRATE PHYLUM KAMPTOZOA (ENTOPROCTA) AND SYNOPSIS OF KAMPTOZOAN DIVERSITY IN AUSTRALIA AND NEW ZEALAND

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Summary

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Kamptozoans are tiny suspension-feeders superficially resembling bryozoans or hydroids, but phylogenetically affiliated with spiralians such as polychaetes. All 150 of the described species undergo budding, either to form clonal aggregations or interconnected colonies. This review provides a synthesis of current knowledge about Kamptozoa, updating the last general English-language description of the phylum provided by Hyman in 1951. Kamptozoan morphology, reproduction, and phylogenetic relationships are characterized. Finally, each of the three major kamptozoan families is described with examples drawn from Australia and New Zealand. Currently 37 species are known from this region, but many more remain to be discovered. The Australian fauna is unusually rich and varied and includes the world's largest kamptozoan species.

Introduction

Kamptozoans are tiny, tentaculate suspension feeders that live in all oceans of the world. Clonal aggregations of independent zooids (Fig. 1a) are found on invertebrate hosts, while colonies of interconnected zooids (Fig. 1b, c) grow on various substrata. Each zooid has the shape of a wine glass: a bowl-shaped calyx is supported by a slender, flexible stalk that attaches basally to the substratum. The calyx is ringed by a horseshoe of ciliated feeding tentacles and contains a U-shaped gut, a small ganglion, a pair of protonephridia and one or two pairs of gonads. The space enclosed by the tentacles forms an atrium, the deepest part of which serves as a brood chamber for developing embryos.

Kamptozoan zooids actively bend and twist. Their characteristic motion is reflected in the phylum's scientific name (Greek: *kamptestai* = to bend) and its common name, "nodding heads". Another name for the phylum, Entoprocta, is less appropriate because it suggests an affiliation with the Ectoprocta (Bryozoa) and it implies erroneously that the anus is completely enclosed by the tentacular ciliation. Kamptozoans bear only a superficial resemblance to bryozoans, with which they were once grouped. Developmentally, kamptozoans are spiralians but their phylogenetic relationships to other metazoans remain enigmatic.

About 150 species have been described worldwide but kamptozoan diversity probably exceeds 500 species (Nielsen 1989). While they are widespread and are quite abundant in some microhabitats, most of the world's kamptozoans are poorly characterized or not known at all, because most species are tiny and easily overlooked. Kamptozoans occur in all oceans, from the intertidal zone to several hundred metres depth. A few colonial species live in brackish water, and one in freshwater. Representatives of all three major families (Loxosomatidae, Pedicellinidae, Barentsiidae) have been found in every marine region that has been thoroughly surveyed. The fourth family (Loxokalypodidae) has been found only once, in the northeastern Pacific.

The main purpose of this review is to synthesize current knowledge about the Kamptozoa. The last general English-language description of this phylum was provided by Hyman (1951), and there have been many advances in our understanding since that time. In summarizing what is known about kamptozoans, I draw heavily on work by two recent pioneers in kamptozoology, P. Emschermann (e.g. Emschermann 1972, 1982) and C. Nielsen (e.g. Nielsen 1971, 1996; Nielsen and Jespersen 1997). A second objective of this review is to highlight the rich and unusual kamptozoan fauna of Australia and New Zealand.

History of study

Kamptozoans were first illustrated by Ellis (1756). Pallas (1774a, b) described the first species as *Brachionus cernuus*, placing it in a genus of rotifers. The same species was placed in the new genus *Pedicellina* by Sars (1835), who considered it a naked bryozoan. Van Beneden (1845) contributed the first thorough monograph of kamptozoan morphology and reproduction. The genus *Urnatella* was described by Leidy (1851) and *Loxosoma* by Keferstein (1862). Allman (1856) pointed out the uniqueness of kamptozoan calyx and tentacle structure. Nitsche (1870) conceived of *Pedicellina*,

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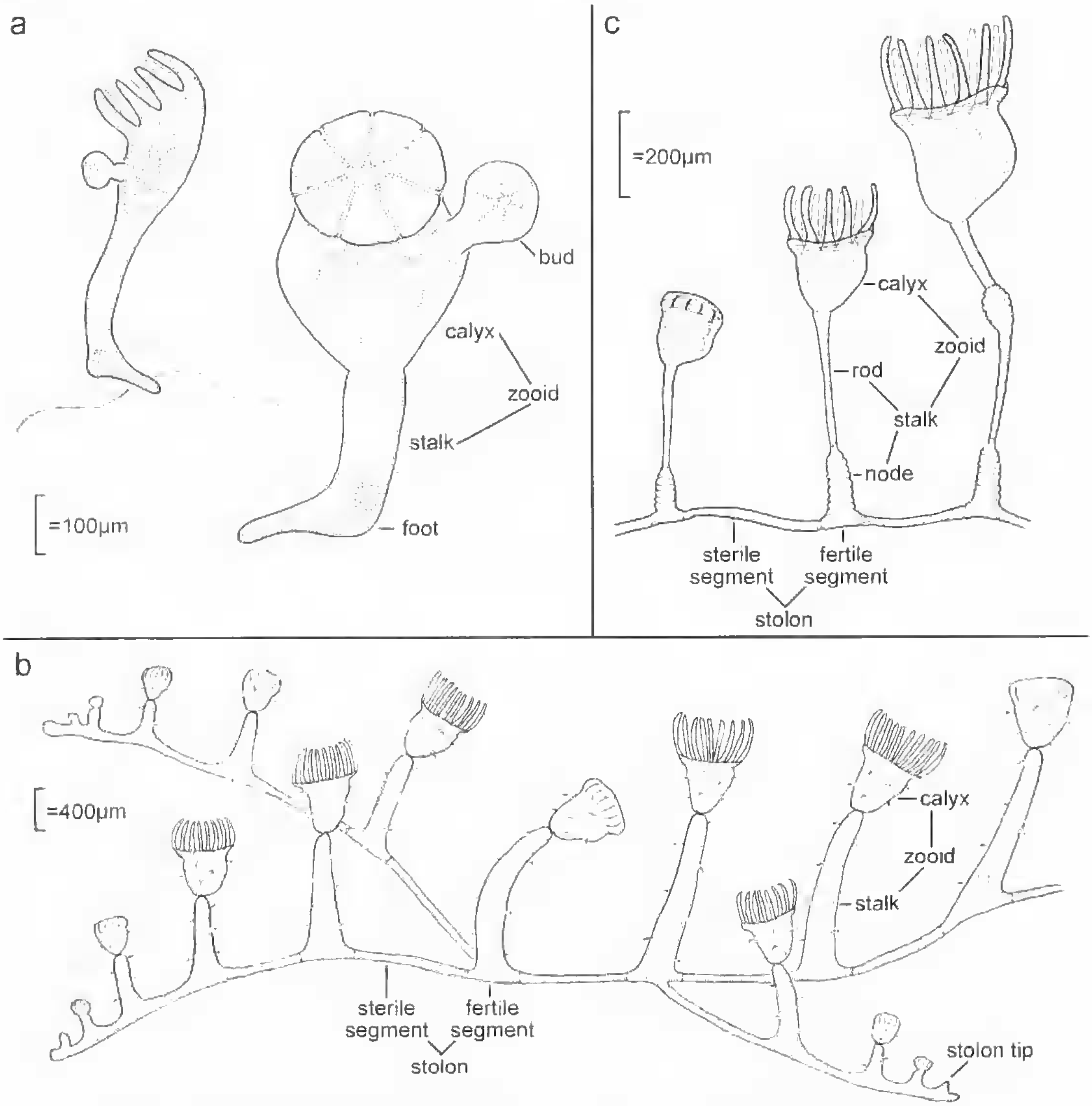

Fig. 1. Structure of kamptozoan zooids. (a). *Loxosomella* sp. 3 on sponge. (b). *Pedicellina whiteleggii*. (c). *Barentsia* sp. 1.

Urnatella and *Loxosoma* as a natural grouping, the Entoprocta, and separated them from all other bryozoans, the Ectoprocta. Hatschek (1888) first raised the entoprocts to the level of phylum. Clark (1921) proposed the name Calyssozoa to distinguish this phylum further from the bryozoans; Cori (1929) agreed with this intent, but changed the name to Kamptozoa, since the name Calyssozoa had already been applied to another taxon (the cnidarian Stauromedusae). Late in the 19th century, a number of prominent scientists investigated kamptozoans, emphasizing embryological and phylogenetic questions (e.g. Barrois 1877; Harmer 1885; Seeliger 1890). Since then, only a few researchers at any one time have focused on kamptozoans.

Morphology and physiology

External characteristics

Kamptozoan zooids are generally constructed of a stalk, basal attachment and calyx (Fig. 1). The height of individual zooids ranges among species from 0.3-30 mm. The stalk develops as an outgrowth of the calyx to form a flexible, roughly cylindrical support. Clonal forms (Family Loxosomatidae) have a specialized basal organ (either a muscular suction

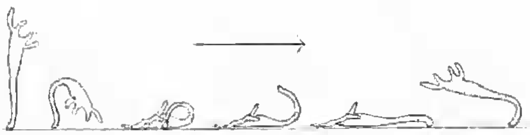

Fig. 2. Locomotion of *Loxosoma agile*. Modified from Nielsen (1966).

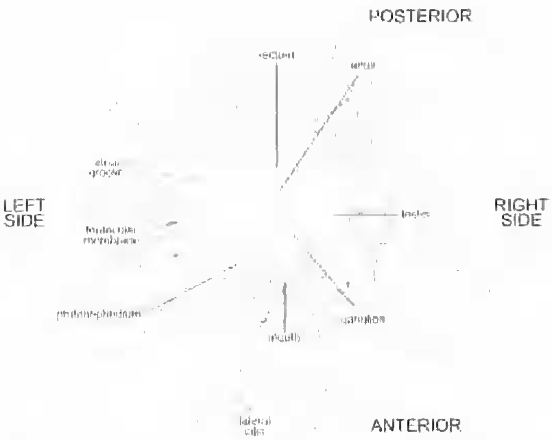

Fig. 3. Diagrammatic top view of a pedicellinid calyx.

disc or a differentiated "foot" with an associated gland (Fig. 1a)) with which they attach to invertebrate hosts. Beneath the stalks of most colonial forms (Families Pedicellinidae and Barentsiidae), stolons (Fig. 1b, c) adhere to various living and non-living substrata with cuticular adhesions. The cup-like calyces range in height from 0.2-1.2 mm and are ringed by a horseshoe of tentacles. The mouth and anus are at opposite sides of the calyx, regarded as anterior and posterior respectively (Figs 3, 4b). The calyx is bilaterally symmetrical; a vertical plane through mouth and anus divides the calyx into right and left mirror images (Fig. 3). The region above the stomach is ventral (this region was below the stomach in the larva); the bottom of the calyx and stalk are dorsal (Fig. 4b).

Body wall, musculature and support

The body wall is a single-layered epithelium, covered by a glycoprotein cuticle containing a trace (0.06-0.45%) of chitin (Jeuniaux 1982) but no collagen (Emschermann 1982). The cuticle is generally thickest on the stalk, which may be darkly pigmented, moderately thin and transparent on the calyx, where the internal anatomy can be readily

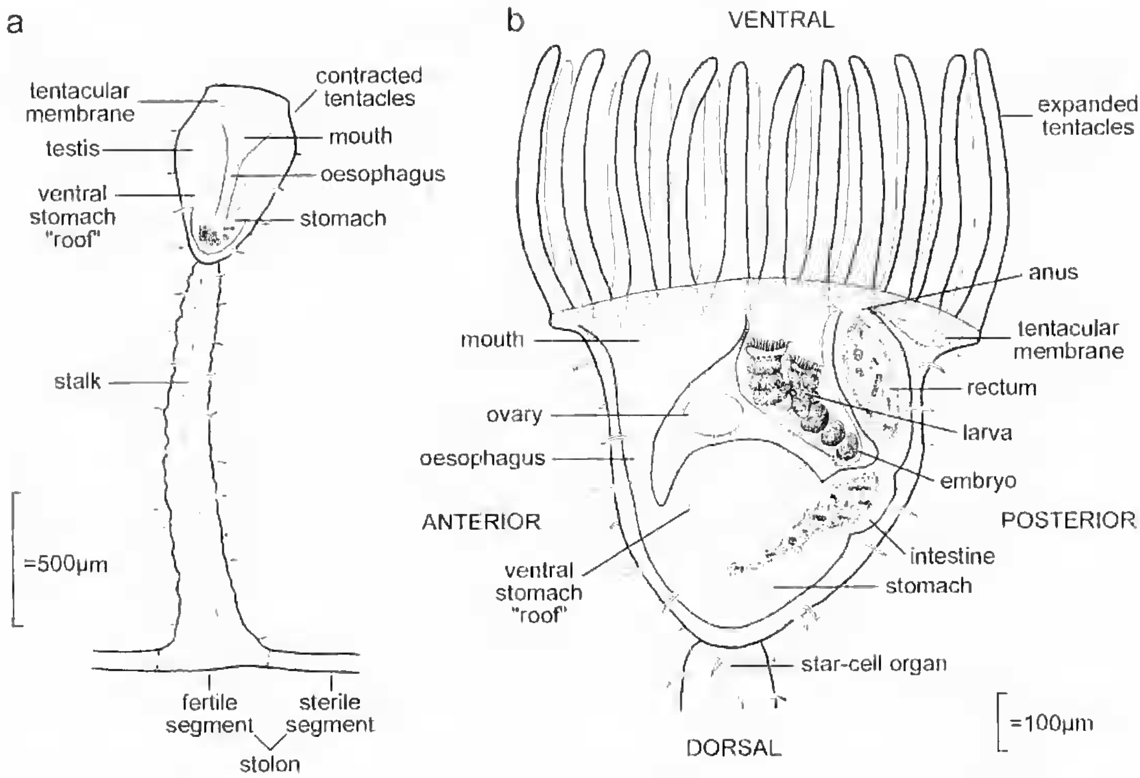

Fig. 4. Structure of a kamptozoan calyx. (a). Anterior view of contracted male *Pedicellina whiteleggii* zooid. (b). Side view of expanded female *P. whiteleggii* calyx.

observed through the body wall, and thinnest on the inner (frontal) side of the tentacles (Nielsen & Jespersen 1997).

Strong longitudinal muscle fibres beneath the stalk epithelium produce the characteristic bending motions of kamptozoan zooids. Circular muscles are limited to the tentacular membrane and sphincters between parts of the gut. The structure of muscle fibres has been described by Emschermann (1969b, 1982), Reger (1969) and Nielsen and Jespersen (1997). Kamptozoans lack a coelom. The cavity surrounding the calycal organs and extending into the tentacles and stalk is filled by a loose fluid matrix of mesenchyme cells which acts as a hydrostatic skeleton and, together with the cuticle, lends the stalk rigidity (Brien 1959).

Locomotion and movement

All kamptozoans have larvae that swim or creep by ciliary action. While larvae represent the main dispersal mode for most colonial, and perhaps many solitary species, some species are mobile at other stages in the life-cycle. In some loxosomatid species, newly released, asexually produced buds can swim with their stalk forward, propelled by their tentacular cilia; in a few loxosomatids, adults may also be capable of such swimming (Atkins 1932; Ryland & Austin 1960; Nielsen 1966). In loxosomatid species whose adults can attach repeatedly to the substratum, passive drifting of detached zooids may also serve for dispersal. Most colonial forms are sessile as adults, but in the freshwater species *Urnatella gracilis* Leidy 1851, short propagation stolons of two or three zooids often break from a larger colony, leading to rapid colonization of a favourable area by fragments of the same original colony which have spread by drifting (Emschermann 1987).

In some species in the genus *Loxosoma*, zooids employ their basal suction discs to somersault across the substratum (Assheton 1912; Nielsen 1964), "moving...in a manner fascinating and unique by a series of gymnastic efforts, which combine the agility of the kangaroo and the deliberation of a geometer caterpillar" (Assheton 1912). The zooid bends down until the calyx attaches by four long oral tentacles to the substratum; the suction disc then detaches from the substratum and flips over the calyx to reattach some distance from its original site; the zooid then returns to an upright orientation (Fig. 2).

While adult locomotion occurs in only some species, the non-locomotory bending motions of attached zooids are characteristic of all members of the phylum. Although the rapid and vigorous nodding of kamptozoans immediately catches the observer's eye, the mechanisms and stimuli involved have not been thoroughly examined. Bending of the stalk results from shortening of longitudinal muscles on one side (Brien 1959). A stronger bending response is obtained by stimulation of calyces than of stalks (Cori 1936). The nodding and writhing may help zooids escape predators, may diminish overgrowth by fouling organisms, or may prevent the calyces from repeatedly filtering the same water.

Finally, individual calyces have a characteristic response to disturbance. When irritated, the tentacles curl inwards and are enclosed by a delicate layer of tissue, the tentacular membrane (Figs 3, 4), which tightens like a draw-string purse by means of circular musculature. This inrolling of the tentacles resembles the contraction of a sea anemone more than the retraction a bryozoan lophophore.

Feeding and digestive system

Kamptozoans are suspension feeders on phytoplankton and other particulate food. Each tentacle has five longitudinal rows of ciliated cells (Atkins 1932; Mariscal 1965; Nielsen & Rostgaard 1976). On the sides of each tentacle (Fig. 3), large lateral cells bear compound cilia that beat towards the tentacle's frontal midline (Nielsen & Rostgaard 1976); these cilia generate the feeding currents. Water is drawn between the tentacles from below the tentacular crown, then sent upward away from the calyx (Atkins 1932). The lateral cilia also capture particulate food from the water currents they create; kamptozoans employ a downstream collecting mechanism (Nielsen & Rostgaard 1976). Inside the rows of lateral cells, rows of narrow laterofrontal cells bear short cilia that presumably transfer food from lateral to frontal cilia (Mariscal 1965). The frontal midline of each tentacle has a single row of large frontal cells bearing short cilia and small mucus vesicles; these cilia beat with the effective stroke towards the base of the tentacle, and transport captured particles in a band of mucus to the base of the tentacles (Nielsen & Rostgaard 1976). Food particles then travel in ciliated gutters, the right and left atrial grooves (Fig. 3) to the mouth (Atkins 1932).

Some kamptozoans apparently trap ciliates and other organisms by rapidly contracting the tentacular crown (Atkins 1932). One Antarctic kamptozoan has special multicellular extrusive organs ("lime-twig glands") that discharge hollow, sticky threads, presumably to capture larger prey items that supplement its diet of suspended particles (Emschermann 1993b).

Kamptozoans have a U-shaped gut, with both the mouth and anus opening ventrally (Figs 3, 4b). The digestive tracts of larvae and adults are simple tubes of ciliated epithelium divided into four regions, and have been characterized by Beck (1938) and Nielsen and Jespersen (1997). The crescent-shaped mouth (Fig. 3) leads to a funnel-like buccal cavity, then to a narrow oesophagus that opens into a voluminous stomach filling much of the calyx (Fig. 4b). Ingested particles are embedded in strands of mucus that are kept in constant rotation by cilia in the stomach: the gut lacks musculature except at sphincters between regions and food is transported entirely by ciliary action (Becker 1938). The strands gradually consolidate into clumps as they pass towards the intestine. Digestive enzymes are secreted by glandular cells in the ventral "roof" of the stomach; absorption occurs both in this region of the stomach and in the intestine (Becker 1938). The stomach leads to a short intestine, and then to the rectum, which projects above the floor of the atrium (Figs 3, 4b), such that faeces released into the tentacular water current are swept away from the calyx. When the tentacles are contracted, the rectum folds lid-like over the atrium.

Circulatory and respiratory systems

Since kamptozoan calyces are tiny, diffusion is a sufficient transport mechanism; no special organs facilitate circulation within the calyx. Loose mesenchyme surrounding the organs allows for the free circulation of dissolved gases and nutrients. Contrary to earlier indications (e.g. Hyman 1951), there are no free amoebocytes enhancing nutrient transport within the mesenchyme matrix (Emschermann 1969a). In loxosomatids, fluids also pass freely between the calyx and the stalk, helped on their way by muscular movements. In many colonial kamptozoans, diffusion may not suffice for circulation throughout the zooid because the stalk is often much longer than in loxosomatids and is partly separated from the calyx by a cuticular septum. Pedicellinids and barentsiids have a circulatory structure, the star-cell organ (Emschermann 1969a). A stack of flattened, stellate cells spans the narrow zone between the stalk and calyx (Fig. 4b). The topmost cell contracts and expands like a pipette-bulb; rhythmic pulsations of the stacked cells pump fluids between calyx and stalk (Emschermann 1969a).

Excretion

A pair of flame-bulb protonephridia, located just posterior of the oesophagus (Fig. 3), apparently functions mainly in ion regulation and osmoregulation (Emschermann 1982). Each protonephridium is composed of four multiciliated cells. Two of the cells form a terminal organ, with a filtration area where they interdigitate; the third and fourth cells encircle the nephridial lumen, and the fourth cell forms the nephridiopore (Franke 1993). In loxosomatid calyces, the two protonephridia open separately into the atrium, while in stolonates they open through a common nephridiopore (Franke 1993). The freshwater kamptozoan *Urnatella gracilis* has a more highly developed excretory system, with 30-40 protonephridia in the calyx, and many others in the stalk (Emschermann 1965).

Excretion of metabolites takes place in the ventral stomach "roof" (Fig. 4), a region that is often eye-catching because it is conspicuously coloured by the pigments of consumed phytoplankton. The large vacuoles of cells in this region contain precipitated uric acid and guanine as well as algal pigments (Becker 1938; Emschermann 1965). These intracellular inclusions are eventually expelled into the stomach and voided.

Nervous system and sense organs

A large, dumbbell-shaped ganglion lies ventral to the stomach, just posterior to the protonephridia (Fig. 3). Nerves radiate from this subenteric ganglion to the tentacles, to other parts of the calyx, and to the stalk. Many kamptozoans have unicellular tactile receptors on the tentacles and on the surface of the calyx (Nielsen & Rostgaard 1976). In addition, loxosomatids often have a pair of lateral sense organs consisting of ciliated papillae on the right and left sides of the calyx. There are no nervous connections between zooids in a colony; earlier suggestions (Hilton 1923) of an interzooidal nervous system have been rejected (Emschermann 1982).

The larvae of many loxosomatids have a pair of eyes, each consisting of a cup-shaped pigment cell, a lens cell and a sensory cell. The structure of the eye is unusual in that light enters perpendicular to, rather than parallel to the long axes of the sensory cilia (Woollacott & Eakin 1973). No adult kamptozoans are known to have eyes but zooids of some species contract in response to sudden exposure to bright light (Emschermann 1982).

Reproduction and development

Asexual reproduction

All kamptozoans grow by budding. In loxosomatids, which live on other invertebrates, buds form in two anterior or anterolateral regions of the calyx, often roughly level with the top of the stomach (Figs 1a, 5a, b, 8a, b). Buds may be produced alternately or simultaneously at the two budding sites. The basal part of the bud's stalk develops an attachment organ. The bud may remain attached to its "parent" for some time, feeding and even becoming sexually mature, but it eventually breaks away, often attaching to a nearby spot on the invertebrate host.

Colonial kamptozoans also bud at the anterior face of zooids, but budding occurs earlier in the life of zooids than in loxosomatids (Brien 1959). The zooids producing buds are often themselves still tiny

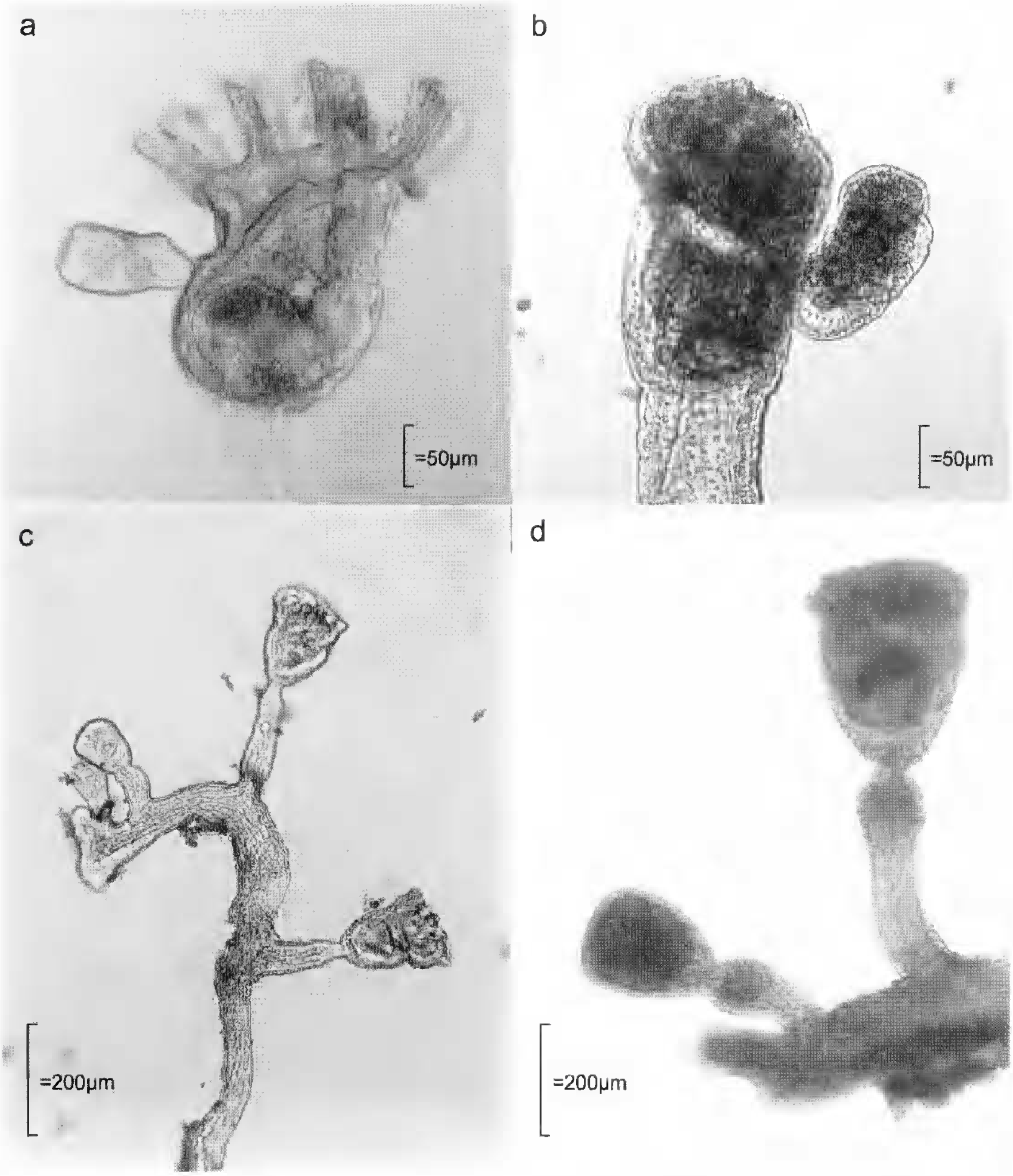

Fig. 5. Asexual reproduction. (a). Calyceal budding in *Loxosomella* sp. 5. (b). Calyceal budding in *Loxosoma* sp. 1. (c). Budding at the stolon tip in *Barentsia matsushimana*. (d). Budding at the stolon tip in *Pedicellina pyriformis*.

buds; each stolon tip is a bud primordium forming anterior to the next youngest bud (Figs 1b, 5c, d). As the buds grow and differentiate into fully formed zooids, they are separated by intercalating growth of the stolon. Eventually this growth ceases and a septum with a central opening forms on each side of the zooid, partitioning the stolon into fertile (zooid bearing) and sterile (without zooids) segments (Figs 1b, c, 4a). Because of this pattern of formation, the anterior side of every zooid along a stolon faces the growing stolon tip. Colony form can be more complex in some barentsiids, which bud from specialized stalk regions. In some species, resting buds (hibernacula) are formed at stolon tips. These undifferentiated buds are enclosed in single or multiple chambers and are covered by a thick cuticle. They germinate only after the stolonic connection to the rest of the colony is severed, and following exposure to low temperatures (Toriumi 1951; Emschermann 1961, 1982).

Pedicellinids and barentsiids, unlike most loxosomatids, can regenerate calyces. Old calyces degenerate and are shed and are replaced by a budding process at the apical stalk tip comparable to that at stolon tips. Injured barentsiid zooids can regenerate new calyces and stalks even from basal stalk and stolon remnants (Hyman 1951; Brien 1959; Mukai & Makioka 1978).

Patterns of bud formation at the histological level are very similar in all kamptozoans (Seeliger 1889, 1890; Brien 1959). An epidermal proliferation of the anterior body wall of a zooid results in an evagination that forms the bud primordium. Budding is essentially an ectodermal process; while some mesenchyme cells migrate from the "parent" into the bud, no endoderm is contributed. At the apex of the bud primordium, an invagination forms, then constricts into an upper and lower vesicle, which become the atrium and the digestive tract, respectively. A narrow passage connecting the vesicles becomes the mouth, while the anus breaks through at a later stage. A constriction soon separates calyx and stalk and the latter elongates. Eventually the atrial cavity breaks through, freeing the tentacles, and the bud begins to feed.

Sexual reproduction

Most loxosomatid calyces are protandric, with a discrete male phase followed by a female phase (Nielsen 1971; Emschermann 1993a); calyx gonochorism has also been reported (Harmer 1915; Prenant & Bobin 1956). Barentsiid calyces are typically gonochoric (Wasson 1997). Some barentsiid colonies are gonochoric, too, containing calyces of only one sex; other barentsiid colonies are simultaneously hermaphroditic, with both male and female calyces formed along the same stolon (Mukai & Makioka 1980; Emschermann 1985; Wasson 1997). A very few barentsiid species have simultaneously hermaphroditic calyces (Johnston & Angel 1940; Wasson 1997). Some pedicellinids have gonochoric calyces in gonochoric colonies (Marcus 1939); others have gonochoric calyces in simultaneously hermaphroditic colonies (Dublin 1905); still others have simultaneously hermaphroditic calyces (Brien 1959; Emschermann 1985).

The reproductive system is rather simple in both sexes. Gonad rudiments derived from mesenchymal cells first appear above the stomach as a pair of tiny oval translucent vesicles (Mukai & Makioka 1980). These grow into large ovoid sacs, consisting of a one-layered epithelium which is the germinal layer from which the gametes arise (Brien 1959). In simultaneously hermaphroditic calyces, a pair of testes lies posterior to the pair of ovaries. Each gonad feeds into a gonoduct, and the right and left gonoducts merge at the ventral midline to open through a common gonopore posterior to the ganglion (Brien 1959).

The testes grow rapidly and may fill much of the calyx (Figs 3, 4a). The spermatozoa have elongate heads (Emschermann 1982; Franzen 1983b). Spawning has rarely been observed; apparently a cloud of sperm is released following a sudden contraction of the calyx (Dublin 1905).

All kamptozoans brood their embryos and release fully formed larvae. The ovaries remain much smaller than the testes (Fig. 4b), with only a few germinal cells at any one time differentiating into oocytes. The small (40-80 µm) but yolky eggs (Franzen 1983a) are fertilized in the ovary, then discharged into the deepest part of the atrium, the brood chamber (Cori 1936; Marcus 1939; Mukai & Makioka 1980). A glandular region of the oviduct secretes a pliant envelope, which encloses the embryo and extends into a cord which tethers it to the floor of the brood chamber (Marcus 1939; Brien 1959). The ovaries release one or a few eggs per day in alternation, the youngest embryos pushing the older ones farther from the gonopore (Brien 1959). The tethered embyros, like a varied bouquet of balloons, can occupy a substantial portion of their mother's calyx (Fig. 4b). The brood chamber contains many embryos in a regular succession of stages from cleaving eggs to contractile larvae. When larvae hatch out of their envelopes, they remain attached to the atrial wall by the cord, with their mouth and ciliary band upward, allowing them to feed on particles in their mother's current (Brien 1959; Mariscal 1965). Swimming larvae are released about a week after fertilization (Mukai & Makioka 1980).

Embryology and development

Kamptozoans show typical spiralian, determinate development (Barrois 1877; Hatschek 1877; Harmer 1885; Lebendinsky 1905; Marcus 1939; Malakhov 1990). Cleavage is spiral and the 4d cell is a mesentoblast cell that proliferates loose mesenchyme in the interior of the embryo, eventually giving rise to the muscles (Marcus 1939). The arrangement of cells at the animal pole resembles an annelidan rather than a molluscan cross (Marcus 1939). The larval mouth forms very near to the anterior margin of the blastopore, which eventually closes; the anus forms secondarily as well. There is never any hint of coelom formation (Marcus 1939).

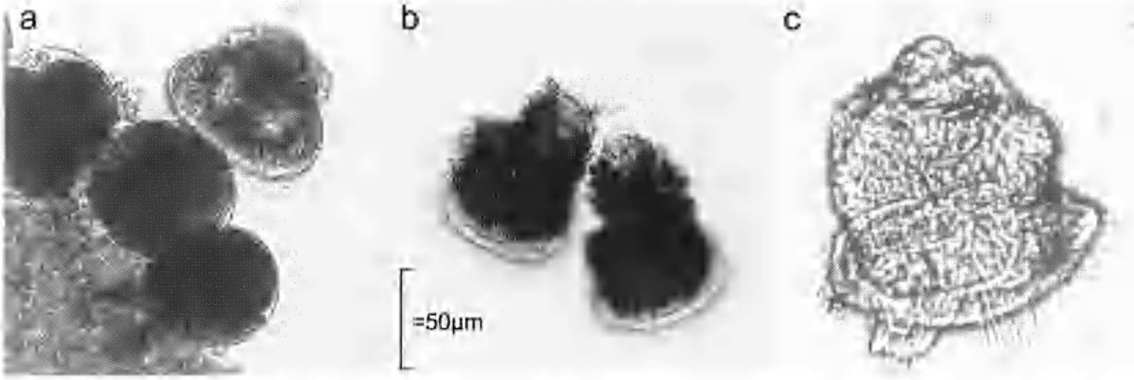

Fig. 6. Tholophores. (a). Embryos and larvae of *Loxosomella* sp. 1. (b). Larvae of *Pedicellina whiteleggii*. (c). Larva of *B. gracilis* var. *simplex*. All figures to same scale.

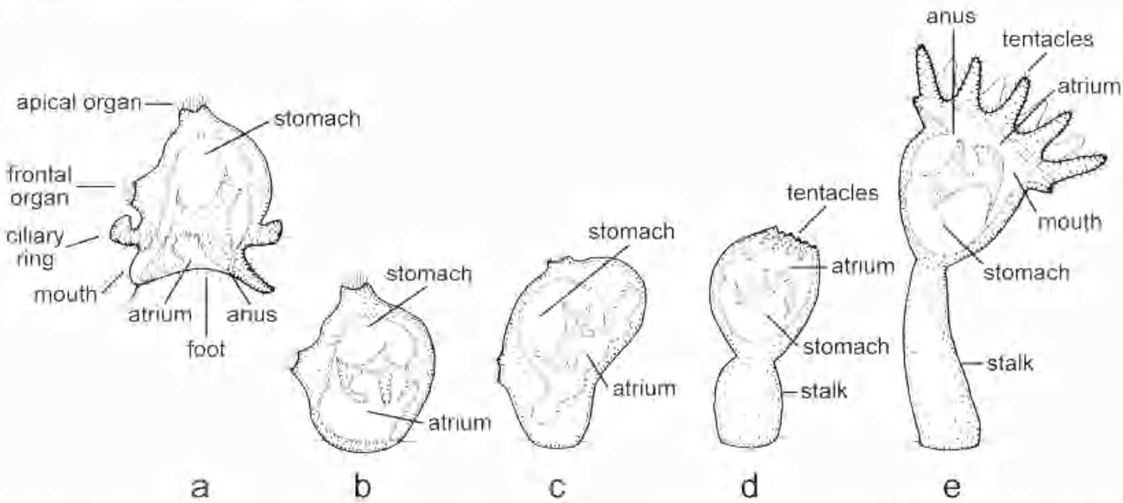

Fig. 7. Schematic representation of metamorphosis in *Pedicellina cernua*. (a). Swimming larva. (b). Newly settled larva. (c). Period of vigorous anterior growth. (d). Zooid with separation between stalk and calyx; tentacles forming. (e). Feeding zooid. Modified from Cori (1929).

Kamptozoan larvae are generally hat-shaped (Figs 6, 7a). Salvini-Plawen (1980) suggested the name tholophora (Greek: *tholos* = dome; *tholia* = straw hat) for them. There are a number of detailed descriptions of larvae (e.g. Barrois 1877; Cori 1929; Marcus 1939; Mariscal 1965; Nielsen 1971) from various regions of the world. The hyposphere of the larva is deeply indented into the prominent, hat-like episphere when the larva is swimming. The curve of the U-shaped gut is in the upper part of the hat; mouth and anus open on the ventral surface (Fig. 7a). There is an apical organ at the top of the hat, a frontal organ at the front of the hat, and a ring of long compound cilia around the brim, just above the mouth (Figs 6, 7a). Below (ventral to) the mouth, there is a second band of shorter compound cilia in the shape of a horseshoe, with the opening of the horseshoe at the anus; the band is also broken behind the mouth. These two ciliary bands beat in opposition and capture particles that are then transported to the mouth by short cilia in the atrial grooves, which run between the two bands of longer cilia from anus to mouth on both sides, as in the adults (Fig. 3). Often there is a ciliated creeping foot in the ventral area between mouth and anus (Fig. 7a). Some tholophores show unusual features (stalked vesicles, a spiderweb pattern of ornamentation, an adhering layer of detritus, etc.) that are not yet understood (Nielsen 1971).

Tholophores resemble the trochophores of some spiralians (Balfour 1885; Cori 1936; Nielsen 1971, 1995; Emschermann 1982). The downstream-collecting ciliary bands of tholophores are similar to those of trochophores in cell-lineage, structure, and function (Nielsen 1995). The apical organs of tholophores also resemble those of trochophores. But unlike trochophores, most tholophores have a frontal organ and a ciliated foot, and their hyposphere is deeply indented into the episphere when the larva is swimming. A few loxosomatid larvae lack the frontal organ and foot and have a more pronounced hyposphere, thus more strongly resembling trochophores, but these forms are considered derived, not ancestral within the phylum (Nielsen 1971). The strongest resemblance of tholophores is to adult kamptozoan calyces; larva and adult share the same shape, structure of the digestive system, atrium with atrial grooves, and a very similar ciliary feeding mechanism.

Larvae from only a few Australian species are known. One *Loxosomella* larva (Fig. 6a) is elongate in the anterior-posterior axis, with adhering particles and a well-developed foot. The *Pedicellina whiteleggii* Johnston & Walker 1917 larva (Fig. 6b) is tall in the ventral-dorsal axis, covered with a remarkably dense layer of detritus, and lacks a foot (Wasson 1995). The *Barentsia gracilis* larva (Fig. 6c) is relatively big, occupying a large portion of the parental calyx. It is about as high as wide and is free of adherent particles.

Most tholophores appear capable of both swimming and creeping; it is not known to what extent the larval period of most species is pelagic or benthic. Most tholophores are feeding larvae with a functional gut. However, the larval period of many kamptozoans appears to be extremely short - hours to days (Nielsen 1971; Emschermann 1982, Wasson 1998) - so the larva's feeding while still in the brood chamber may be more important than feeding after release. On the other hand, some *Loxosoma* larvae are often caught in the plankton and are presumed to have a long pelagic phase (Jägersten 1964; Nielsen 1966).

Metamorphosis has been carefully described in a few kamptozoan species (Barrois 1877; Harmer 1887; Cori 1936; Marcus 1939; Nielsen 1971; Emschermann 1982). The larva creeps on the substratum, testing it with the frontal organ, before attaching by the region around the frontal organ, settling on the anterior side (loxosomatids) or by attaching by the foot region, settling on the circumference of the retracted ventral ciliary girdle (pedicellinids and barentsiids). The atrium becomes enclosed by a constriction of the episphere dorsal to the ciliary girdle (Fig. 7b). The atrium and digestive tract are rotated upwards as a result of rapid growth of the anterior region of the episphere (Fig. 7c). Next, a separation forms between calyx and stalk and the latter elongates (Fig. 7d). Ciliated tentacles form as ectodermal protuberances at the periphery of the atrium (Fig. 7d), roughly in the location of the degenerating larval ciliary bands. Finally, the atrium breaks open, releasing the tentacles, and feeding begins (Fig. 7e).

While in all colonial and many clonal species the larva does metamorphose directly into the adult, some loxosomatids have precocious budding in which the larva does not metamorphose, but instead dies as the buds it bears grow and are released (Harmer 1885; Jägersten 1964; Nielsen 1971). In effect, the larval bud, rather than the larva itself, is the route to adulthood in these species. In the most extreme cases, the larva is completely consumed by an internal bud that forms while the larva is still within its parent, and the larval gut is absent (Nielsen 1971). Some remarkable species display further heterochrony: the buds themselves already have buds in turn or even are sexually mature while still contained in the larva (Jägersten 1964).

Phylogeny

Fossil record

Kamptozoans fossilized by bioimmuration occur in upper Jurassic rocks in Great Britain (Todd & Taylor 1993) and northern France (J. Todd, pers. comm. 1995). The structure of zooids unambiguously identifies them as members of the extant genus *Barentsia*. These Mesozoic fossils set a minimum time for the divergence of what is probably the most derived family, suggesting that ancestral members of the phylum may date back much further.

Relationships with other invertebrate taxa

Historically, there have been several proponents of a close relationship between kamptozoans and bryozoans (e.g. Harmer 1885; Marcus 1939; Prenant & Bobin 1956; Nielsen 1971, 1995). Zooids of both taxa have a U-shaped gut and are ringed by ciliated tentacles. Budding and hibernacula occur in both taxa and neither has an endodermal contribution from "parent" to bud. In both groups, larval eyespots have sensory cilia oriented at right angles to the incoming light (Woollacott & Eakin 1973). However, many other workers reject a close evolutionary affiliation of kamptozoans with bryozoans (e.g. Allman 1856; Hatschek 1888; Cori 1936; Hyman 1951; Brien 1959; Jägersten 1972; Emschermann 1982). They attribute the similar body plans of adults to common suspension feeding habits and tiny body sizes. Budding and hibernacula are found in many sessile taxa and lack of endodermal contribution to buds is found in pterobranchs and some ascidians as well as kamptozoans and bryozoans. The similarity of the larval eyes is striking but, since the eyes are constructed somewhat differently (Woollacott & Eakin 1973), they are not necessarily homologous.

Beyond ascribing similarities to convergence, opponents of a close relationship between kamptozoans and bryozoans emphasize the differences between the two taxa. Kamptozoans have no coelom; bryozoans do, although it is rather unusual. Kamptozoans have protonephridia and gonads; bryozoans do not (Emschermann 1982). Kamptozoans retract their tentacles by curling them inwards and pulling the tentacular membrane around them; bryozoans retract the whole polypide and the lophophore shuts like an inverted umbrella (Brien 1960). Kamptozoans have downstream-collecting ciliary bands, while bryozoans have upstream-collecting ciliary bands (Nielsen & Rostgaard 1976; Nielsen 1995). A key component of the bryozoan body plan is the box-like cystid, absent in kamptozoans. There is little evidence of communication or nutrient flow between kamptozoan zooids, or of polymorphism among zooids; these features are characteristic of bryozoans (Brien 1960). Kamptozoan nervous systems are limited to single zooids, while bryozoans have colonial nervous systems linking zooids (Emschermann 1982). Kamptozoan metamorphosis usually involves retention of the larval gut and other larval structures; bryozoan metamorphosis is a "catastrophic" reorganization without retention of larval features (Brien 1959). A recent molecular analysis of complete 18S rRNA sequences (Mackey *et al.* 1996) provides further evidence against a close relationship between kamptozoans and bryozoans.

If kamptozoans are not closely related to bryozoans, with what group of animals are they allied? Based on embryology (Brien 1959; Nielsen 1971, 1995; Emschermann 1982) and molecular sequence data (Mackey *et al.* 1996), affinities must be sought among other spiralians. Some authors have been impressed by similarities between kamptozoans (especially loxosomatid larvae) and rotifers (Barrois 1877; Harmer 1885; Davenport 1893; Hyman 1951), or turbellarian flatworms (Salvini-Plawen 1980). Haszprunar (1996) proposes a sister group relationship between kamptozoans and molluscs, emphasizing similarities such as a chitinous cuticle, a circulatory system with sinuses, and a ventral, ciliary gliding sole (at some stage in the life-cycle) and a pedal gland. Alternatively, kamptozoans may be more closely allied with annelids (Emschermann 1982). Until further evidence resolves the question, the precise phylogenetic position of kamptozoans remains an enigma.

The similarity between adult kamptozoan calyces and tholophores has led to the proposition that the phylum originated by paedomorphosis. This hypothesis is developed in depth by Jägersten (1972), who envisages the original kamptozoan life-cycle as consisting of a planktotrophic trochophore larva and a benthic creeping adult with a ciliated foot. In this paedomorphic scenario, the original motile adult was eliminated but its ciliated foot was retained by the larva, which became sexually mature. This larva then gave rise to a secondary benthic adult, which retained the same ciliary feeding mechanism as the larva, although the ciliary bands eventually were drawn out on to tentacles. The new adult developed a stalk, an attachment organ, and the ability to bud. Haszprunar *et al.* (1995) recently presented a similar scenario of a paedomorphic origin for the phylum, but beginning with a lecithotrophic larva.

Key to the orders and families

1 (a) clonal: new zooids budded at calyx and then released; musculature continuous between stalk and calyx; star-cell organ absent; larva usually with paired frontal organ ....O. SOLITARIA, F. Loxosomatidae
(b) colonial: new zooids budded at base of older zooids or from stalks and remain connected to each other............................O. COLONIALES; 2

2 (a) zooids connected by non-septate basal plate; musculature continuous between stalk and calyx; star-cell organ absent; larva with paired frontal organ ....Sub.O. ASTOLONATA, F. Loxokalypodidae [known only from North-eastern Pacific]
(b) zooids connected by septate stolon or rarely (*Urnatella*) septate basal plate; musculature not continuous between stalk and calyx; star-cell organ present; larva with unpaired frontal organ ....Sub.O. STOLONATA; 3

3 (a) stalk of zooids with continuous longitudinal musculature, fairly wide throughout whole length, stalk and calyx often with cuticular spines ....F. Pedicellinidae
(b) stalk of zooids alternating between wide muscular nodes and narrow rigid rods; rods often with cuticular pores; stalk and calyx generally without cuticular spines ....F. Barentsiidae

Systematics and Australian diversity

Order Solitaria Emschermann, 1972
Family Loxosomatidae (Hincks, 1880)

The order Solitaria contains only a single family, the Loxosomatidae. Nevertheless, it is the largest natural grouping of kamptozoans, with about 100 of the 150 described species. Three loxosomatid genera are currently recognized (Nielsen 1996): *Loxosomella*, *Loxomespilon*, and *Loxosoma*, and are distinguished primarily by their basal attachment structures. About 20 species of loxosomatids have been reported from Australia and New Zealand but only seven of them are described (Appendix). Many more species certainly remain to be discovered; until

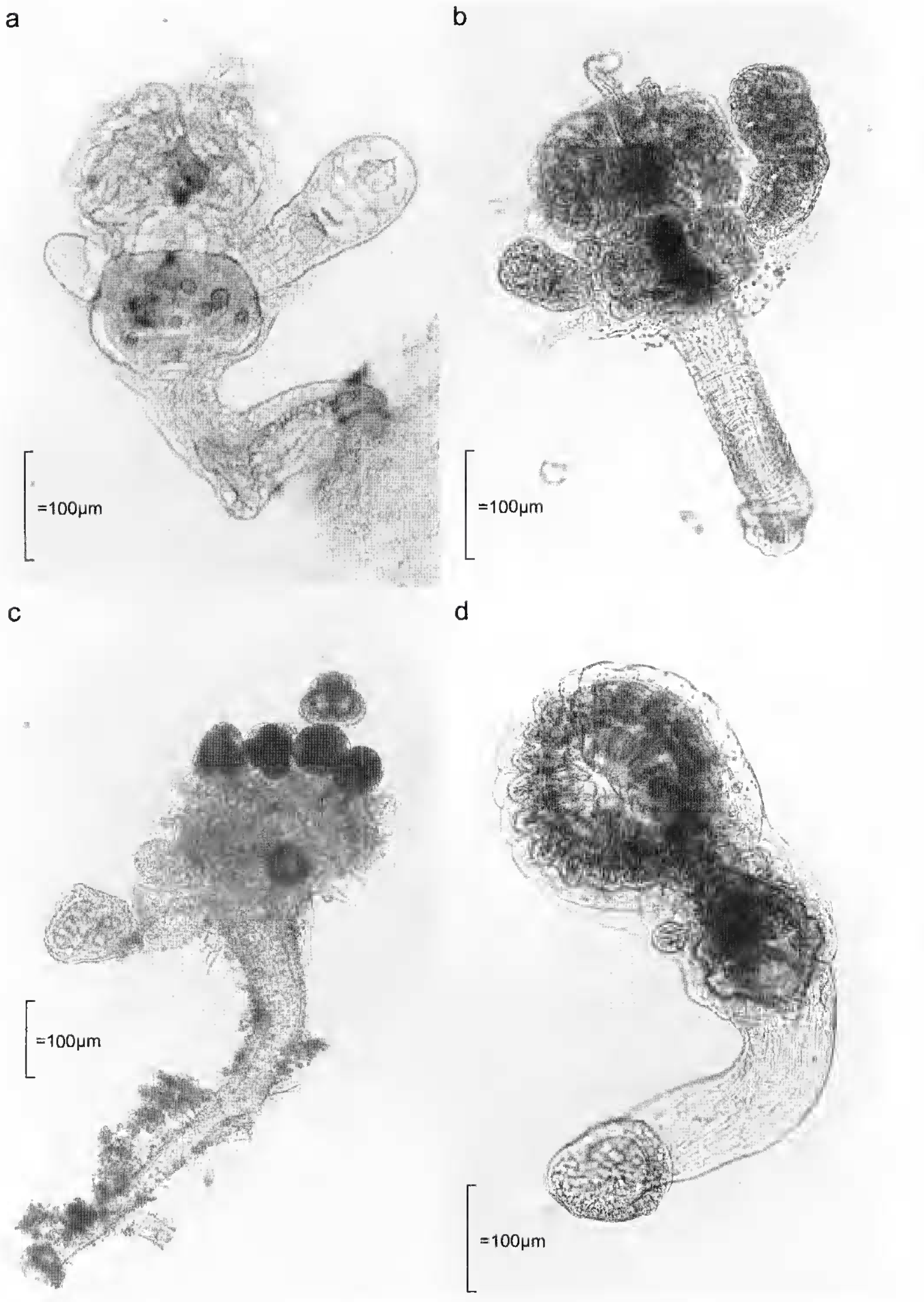

Fig. 8. Loxosomatid diversity. (a). *Loxosomella* sp. 3 showing foot. (b). *Loxosomella velatum*. (c). *Loxosomella* sp. 1 with larvae at top of calyx. (d). *Loxosoma* sp. 2 showing basal muscular disc.

more thorough surveys are undertaken, it is impossible to assess the true diversity Australia's loxosomatids.

Loxosomatids, which form clonal aggregations by calyceal budding, are considered the most plesiomorphic group of kamptozoans (Emschermann 1972). The highly contractile zooids are often very small (less than 1 mm high). Calyx and stalk are not sharply separated and longitudinal musculature is continuous between them. The calyx and tentacles are generally oriented obliquely to the stalk (Figs 1a, 8). The calyces are often compressed in the anterior-posterior axis, sometimes so strongly that the zooids resemble paddles.

In *Loxosomella*, the basal part of the stalk of buds is differentiated into a structure resembling a human foot (Figs 1a, 8a). The heel of the foot is anterior and contains a conspicuous gland. A groove lined by accessory gland cells runs from the heel to the posterior toe, where it opens. When a bud is released from its "parent", it attaches to the substratum by its toe. In some species the zooid retains the glandular foot for its entire existence and is able to detach and reattach repeatedly over its lifetime. In other species, the foot of the bud degenerates after attachment and the adult becomes permanently cemented to the substratum (Figs 8b, c). Zooids of the monotypic genus *Loxomespilon* have a very reduced stalk and foot but otherwise resemble *Loxosomella* zooids (Bobin & Prenant 1953; Nielsen 1996). Seven described and eight undescribed species of *Loxosomella* are known from Australia and New Zealand, and most of the species in the Appendix whose basal attachment structures could not be assessed (and so are listed merely as "Loxosomatid sp.") probably belong to *Loxosomella* as well.

In *Loxosoma*, each zooid is attached by a muscular suction disc at the base of the stalk (Fig. 8d); additional suction discs may occur posteriorly and/or at the base of the tentacles (Nielsen 1996). Zooids retain the ability to detach and reattach, sometimes moving actively across the substratum (Fig. 2). All known *Loxosoma* larvae have stalked vesicles on the episphere and undergo budding rather than a normal metamorphosis (Nielsen 1996). Only three (undescribed) *Loxosoma* species are known from Australia and New Zealand.

Most loxosomatids dwell on other invertebrates. In Australia and New Zealand they have been reported from various sponges, a sipunculan, various polychaetes, two hirudineans, a squat lobster, two prawns, and various bryozoans (Appendix). As more potential hosts in this region are examined for the presence of loxosomatid symbionts, this list will certainly grow. Each loxosomatid species appears to have either a single host species or a limited set of potential host species. Larvae, and possibly also buds and motile adults, can colonize new hosts; it is not known whether propagule preference or differential mortality on different host species is responsible for the later distribution of adults. Association with other invertebrates has clear benefits for the loxosomatid. The zooids are often located in the pathway of the host's feeding or respiratory water currents, which they may use for their own ciliary feeding (Nielsen 1964). The host probably offers the fragile zooids protection from predation or other damage. Whether the presence of loxosomatids negatively affects their hosts is not known; Williams (2000) has shown that host epidermis may be modified by loxosomatid symbionts.

Worldwide, many loxosomatid species (about 50%) live on polychaetes; they are found on or between the parapodia, on the gills, on the setae, or under the elytra of members of ten polychaete families (Nielsen 1989). *Loxosomella diopatricola* Willams 2000 and seven undescribed species of loxosomatids are known from polychaetes in Australia and New Zealand (Figs 5a, b, 8d; Appendix).

While loxosomatid species diversity is highest on polychaetes, loxosomatid density is probably highest on sponges. Loxosomatids may form strikingly dense aggregations on sponges — sometimes 100,000 zooids on a fist-sized sponge (Rützler 1968). Some of these sponge-dwelling forms are unusually darkly pigmented, and an aggregation against the background of a brightly coloured sponge can be eye-catching. Two undescribed species of *Loxosomella* are known from sponges in Australia and New Zealand (Figs 1a, 8a).

Six loxosomatid species in Australia (*Loxosomella breve*, *L. circulare*, *L. cirriferum*, *L. pusillum*, *L. velatum* (all Harmer 1915), *L.* sp. 1) grow on bryozoans (Appendix). Most of these species are ornamented by odd cirriform organs or papillae (Fig. 8b, c), and share other similarities that suggest they comprise a clade; both the ecology and the taxonomy of bryozoan-dwelling species merit further attention. Some bryozoan-dwelling loxosomatids, originally described by Harmer (1915) from *Siboga* expedition material, live in very close association with their hosts. One miniscule loxosomatid species even lives in the compensation sac of its host: almost every compensation sac in an infested bryozoan colony contains a loxosomatid zooid (Harmer 1915).

Order Coloniales Emschermann, 1972

Sub-Order Stolonata Emschermann, 1972

The sub-order Stolonata is the other large natural grouping of kamptozoans and exhibits the second basic body plan within the phylum. The calyces of stolonates are generally larger than those of loxosomatids, with stronger ciliary currents that apparently free the zooids from dependence on hosts' ciliary currents (Emschermann 1972). Stolonate calyces are generally laterally compressed (Fig. 4a v. 4b; Fig. 10a v. 10b) and musculature is reduced, often to just a few longitudinal strands, the atrial retractor muscles, which extend from the base of the calyx to the atrium and serve to depress it (Emschermann 1972). Calyx and stalk are separated by a cuticular diaphragm and the calyx-stalk junction is spanned by the circulatory star-cell organ (Emschermann 1969a); the longitudinal musculature of the stalk is not continuous with that of the calyx. The stalk often bears cuticular pores or spines which vary in size and density with environmental conditions. Stolonate zooids, as their name implies, grow on cylindrical stolons that are usually divided into fertile (zooid-bearing) and sterile (no zooids) segments by transverse septa (Figs 1b, c, 4a). The septa may function to space the zooids, thus avoiding interference in feeding, or may prevent damage by sealing off intact sections from harmed ones.

Stolonate kamptozoans are members of the sessile benthic community and often grow together with hydroids and bryozoans. They are preyed upon by nudibranch molluscs, some of which appear to specialize on barentsiid species (MacDonald & Nybakken 1978); predation by turbellarian flatworms has also been observed (Canning & Carlton 2000). Although seldom conspicuous, stolonate kamptozoans are often fairly abundant. I have found stolonates intertidally at every site surveyed in Australia and New Zealand by collecting various substrata (mostly sponges, ascidians, bryozoans, worm tubes and bivalve shells) in the field and examining them in the laboratory. In some localities, an astounding 50%-75% of all substrata searched were infested with stolonate kamptozoans, although the level was usually about 5-10% at other sites.

Family Pedicellinidae (Johnston, 1847)

The family Pedicellinidae is considered more plesiomorphic than the Barentsiidae (Emschermann 1972): pedicellinid zooids retain a fairly simple zooidal structure, with undifferentiated stalks that have continuous musculature. Five genera are recognized but four of these (*Chitaspis*, *Loxosomatoides*, *Myosoma*, *Sangavella*) contain only one or two species, and have not been reported from Australia or New Zealand. The larger genus *Pedicellina* comprises about twelve species worldwide, six of which are known from Australia and New Zealand (Appendix).

In colder waters of this region, *P. whiteleggii* Johnston & Walker 1917 (Figs 1b, 4a, b, 9c) is ubiquitous and can be collected readily from coastal habitats (Wasson 1995). This species is recognized by its spination, by the distinctive, glistening, double rows of large cells on the tentacles, and by its tall, particle-covered larva (Fig. 6b). In warmer waters, *P. whiteleggii* is replaced by another abundant species, *P. compacta* Harmer 1915 (Fig. 9a), which is characterized by short, squat zooids ornamented with filiform spines (Wasson 1995).

A rarer pedicellinid from Otago, New Zealand, and Tasmania is *Pedicellina pyriformis* Ryland 1965 (Fig. 9b). The stalks grow up to 6 mm high, and calyces can be almost 1 mm high: this species is a giant among the world's pedicellinids. Zooids are also more densely clustered in this species than in other pedicellinids. The wide stolons lack septa; the absence of intervening sterile segments allows zooids to grow very close together along the stolon.

Family Barentsiidae Emschermann, 1972

This family is characterized by the division of the stalk into wide, flexible, muscular nodes and narrow, rigid, non-muscular rods that are often perforated by pores (Figs 1c, 10c, 11c). An incomplete cuticular septum separates each node from the rod above it. There is a minimum of one basal node and one rod apical to it, but many species have multiple alternating nodes and rods, lending a segmented appearance to the stalk.

Five genera of barentsiids are recognized. *Coriella*, *Pseudopedicellina*, *Pedicellinopsis* and *Urnatella* (the sole freshwater form) each contain a single species; most of the roughly thirty known barentsiid species belong to the genus *Barentsia*. Seven barentsiid species are known from Australia and New Zealand (Appendix), six in the genus *Barentsia* and one in the genus *Pedicellinopsis*. The common species of colder waters, *Barentsia* sp. 1 (Figs 1c, 10a, b), is characterized by small, delicate zooids only about 1 mm high, usually with 1-3 series of stalk nodes and rods. In warmer waters, *B.* sp. 1 is supplemented by *B. geniculata* Harmer 1915 (Fig. 10c) which has many (average 4-5) series of stalk nodes and rods. In its segmented stalk structure, *B. geniculata* resembles the cosmopolitan species *B. benedeni* (Foettinger 1887) (found in Australian harbours), from which it can be distinguished by its wider, shorter nodes and by the less pronounced anterior orientation of the calyx.

Pedicellinopsis fruticosa Hincks 1884 (Fig. 11) is a remarkable barentsiid apparently endemic to southern Australian waters (Appendix). Zooids spiral around a hard central stem (Fig. 11a), from which each zooid is separated by a septum. Each stem resembles a tree-fern, with the newest zooids at the apical growing tip; older regions of the stem where zooids have degenerated have spiral patterns of zooid scars as do lower regions of tree-fern trunks. The thick, rigid stems branch, forming bushy

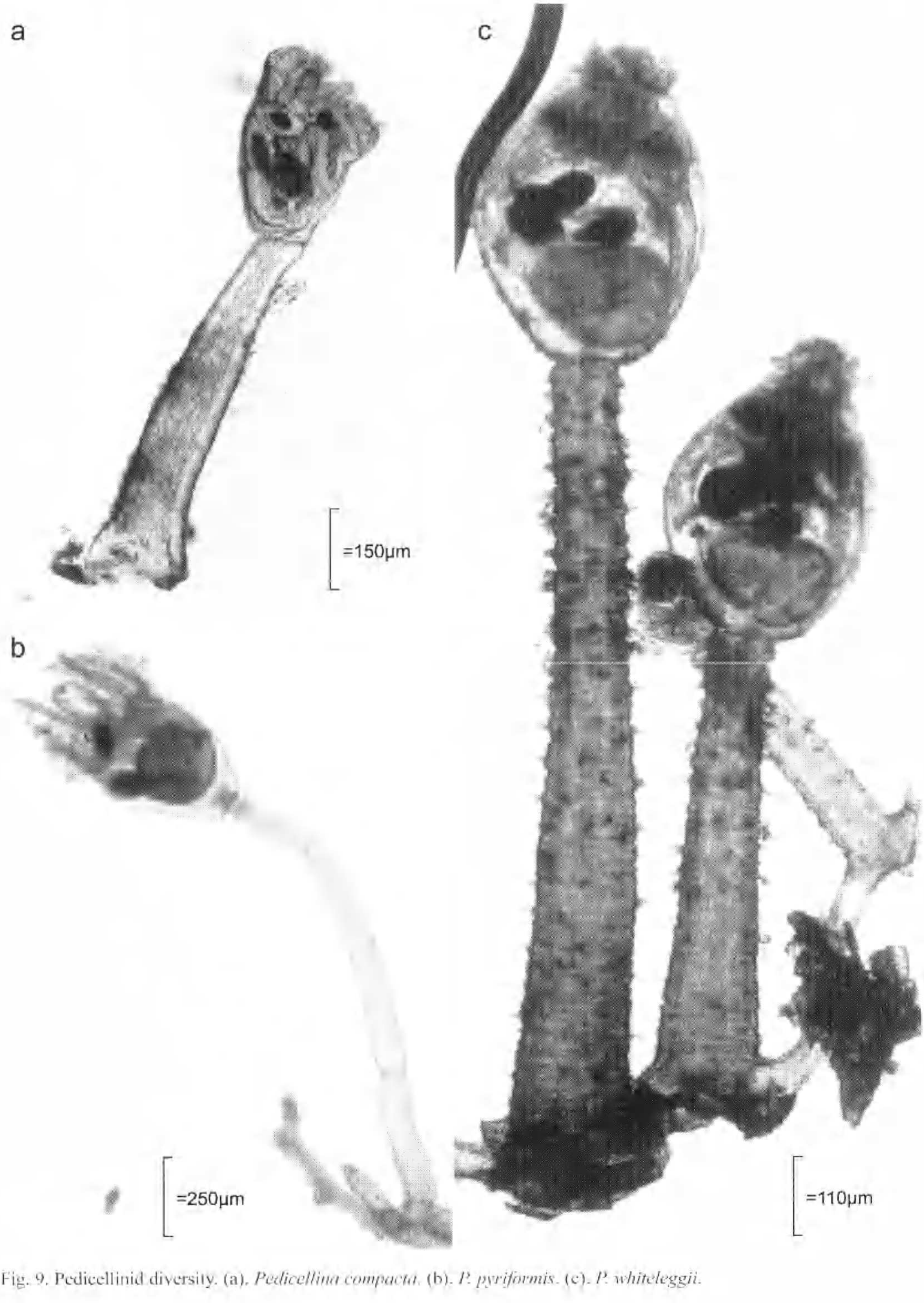

Fig. 9. Pedicellinid diversity. (a). *Pedicellina compacta*. (b). *P. pyriformis*. (c). *P. whiteleggii*.

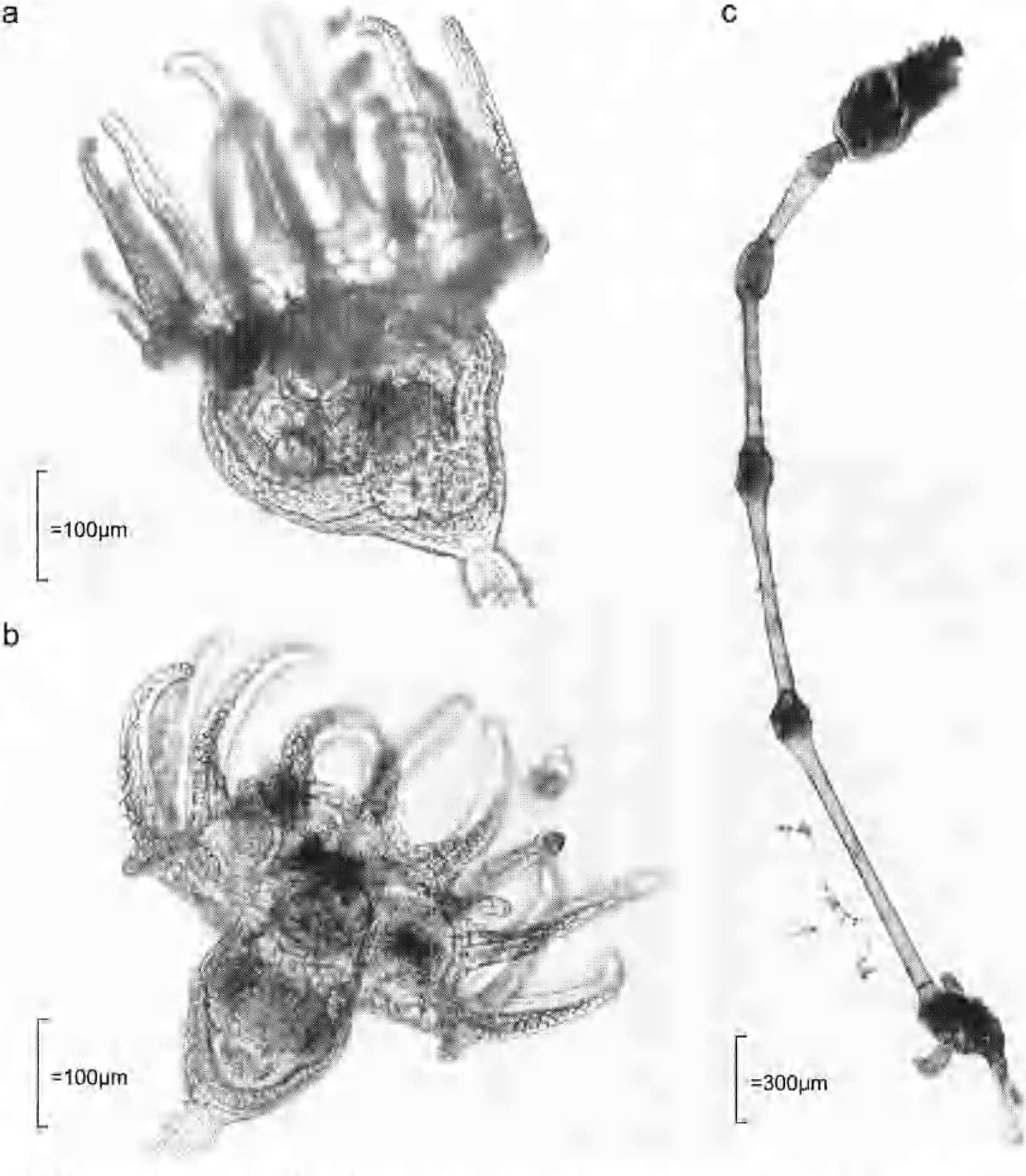

Fig. 10. Barentsiid diversity. (a). and (b). *Barentsia* sp. 1 in side and anterior view, respectively. (c). *B. geniculata.*

colonies that may reach 30 cm across, far and away the record for a kamptozoan. They are anchored to the substratum by a lush basal growth of free stolons, which extend downwards to serve as rhizoids and secondarily back up the stem, becoming intertwined with it. Individual zooids, although unsegmented, grow to a length of 6 mm. The nodes are large and annulate (Fig. 11c). The rods are a deep golden brown due to a very thick cuticle and make a striking contrast to the pale calyces and nodes. The rods are decorated with alternating rows of bubble-like pores and pairs of lateral cuticular ridges (Fig. 11b, c), a pattern of stalk ornamentation not known from any other barentsiid. A large cuticular spine extends up past the stalk-calyx junction on the aboral side of the zooid (Fig. 11b). With its long list of unique features, *Pedicellinopsis fruticosa* may be the most highly derived member of the phylum Kamptozoa. It has yet to be observed alive.

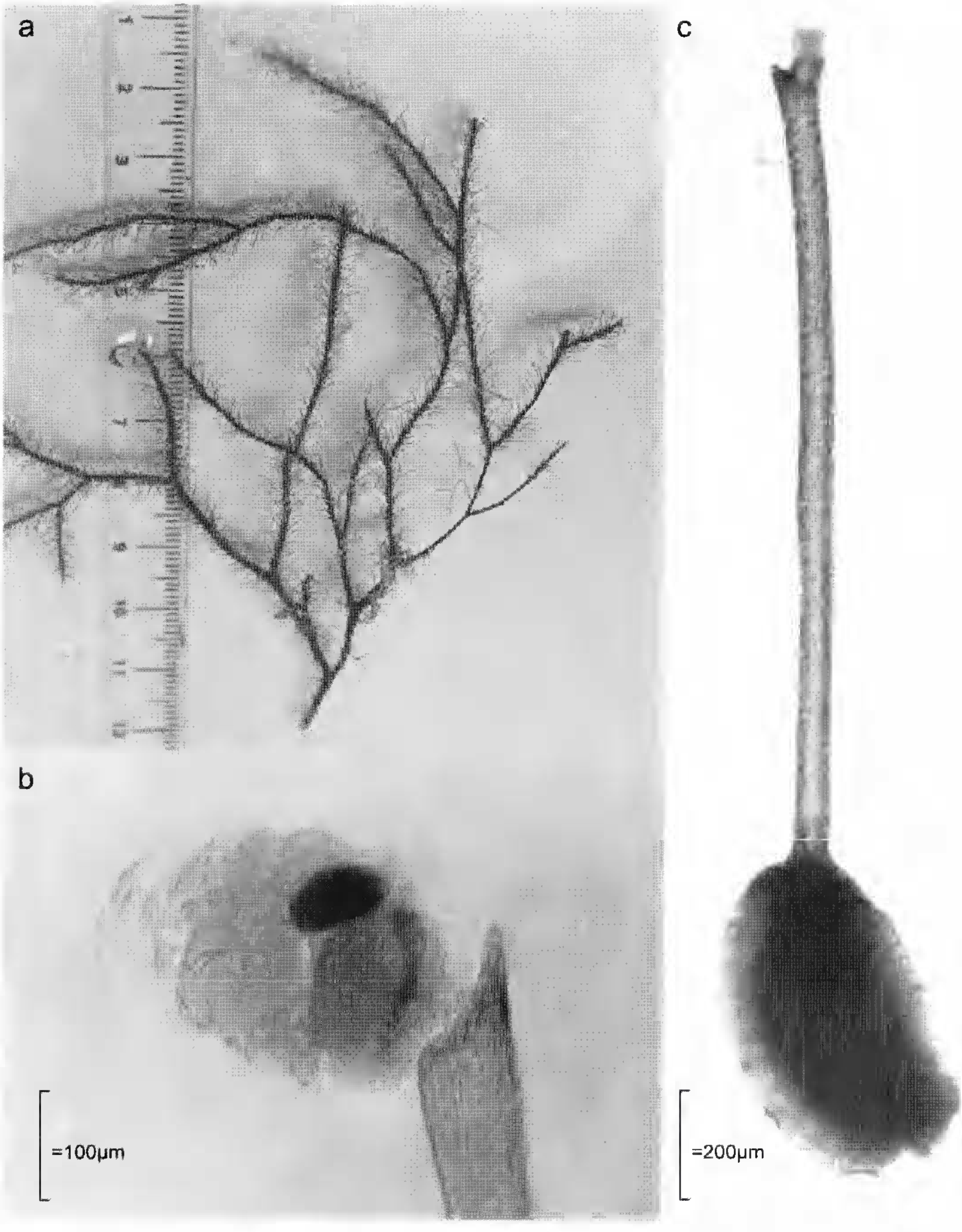

Fig. 11. The barentsiid *Pedicellinopsis fruticosa*. (a). Colony, showing zooids spiraling off of thick main stem. (b). Calyx and posterior spine. (c) Stalk, showing large annulate node and regularly ornamented rod.

Perspectives on the Australian fauna

Reports of kamptozoans from Australian waters are scarce, and currently only about 37 species of kamptozoans are known from Australia and New Zealand (Appendix). However, the Australian kamptozoan fauna is unusually varied, encompassing extremes of the body plan. The world's largest kamptozoan, *Pedicellinopsis* *fruticosa*, dwells in these waters, as do some of the world's smallest kamptozoans, tiny *Loxosomella* species on bryozoan hosts. Australian species may also hold the record for the greatest density of zooids in colonies: *Pedicellina pyriformis* packs in one giant zooid after another along its peculiar non-septate stolon, while in *Pedicellinopsis fruticosa*, zooids spiral around a rigid central stem resulting in a density of zooids and a growth pattern unknown in other kamptozoans.

Kamptozoans in Australia are neither rare nor hard to find. The fauna of Australia is so poorly characterized that new and unreported species (as well as those listed in the Appendix) probably can be collected in only a few hours anywhere along the coast. Beyond taxonomic identity, we know virtually nothing about the biology of Australian species. The little we do know leads us to suspect that further investigations hold much promise for new insights into kamptozoan ecology, symbiotic relationships, larval biology, biogeography and phylogeny. Certainly, given the geographical dimensions and ecological diversity of this country, many new morphological adaptations and life history variations are likely to be revealed when the Australian kamptozoan fauna is more thoroughly examined.

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Appendix

Known kamptozoan diversity in waters around Australia and New Zealand.

This appendix lists the 19 described and 18 undescribed species of kamptozoans known from Australia and New Zealand. The first column gives the species name. Undescribed species have been assigned a number. Those loxosomatids whose basal attachment (generic character) could not be determined are listed simply as "loxosomatid". The second column gives the author of the original species description for described species, or a brief descriptive phrase (for loxosomatids, host is given) for undescribed species. The third column gives the citation for occurrence of this species in Australia or New Zealand. For new records (Wasson, this paper), the name of the collector is given in parentheses. The fourth column lists (abbreviated) the Australian State or the Island of New Zealand where the species was found.

FAMILY LOXOSOMATIDAE (7 described + 17 undescribed species)

Loxosomella breve	(Harmer, 1915)	Hastings 1932	QLD
Loxosomella circulare	(Harmer, 1915)	Hastings 1932	QLD
Loxosomella cirriferum	(Harmer, 1915)	Hastings 1932; Wasson, this paper (R. A. Birtles & P. Arnold)	QLD
Loxosomella diopatricola	Williams, 2000	Williams 2000	VIC
Loxosomella kefersteinii	(Claparède, 1867)	Wasson & Shepherd 1997	SA
Loxosomella pusillum	(Harmer, 1915)	Hastings 1932	QLD
Loxosomella velatum	(Harmer, 1915)	Wasson, this paper (R. A. Birtles & P. Arnold)	QLD
Loxosomella sp. 1	on bryozoan	Wasson & Shepherd 1997	SA
Loxosomella sp. 2	dark zooids on sponge	Wasson & Shepherd 1997	SA
Loxosomella sp. 3	light zooids on sponge	Wasson, this paper (M. Barker & K. Wasson)	SNZ

Loxosomella sp. 4	on polychaete *Sthenelais*	Hastings 1932	QLD
Loxosomella sp. 5	on polynoid polychaete	Wasson, this paper (M. Barker & K. Wasson)	SNZ
Loxosomella sp. 6	on prawns	Wasson, this paper (R. Lester)	NT
Loxosomella sp. 7	on polychaete	Wasson, this paper (D. Gordon)	NNZ
Loxosomella sp. 8	on polychaete *Eunice*	Williams 2000	VIC
Loxosoma sp. 1	on polychaete *Copperingeria*	Haswell 1891; Hastings 1932; Wasson, this paper (R. A. Birtles & P. Arnold)	QLD QLD
Loxosoma sp. 2	on polychaete *Pectinaria*	Wasson, this paper (J. Collins)	QLD
Loxosoma sp. 3	on polychaete *Axiothella*	Wasson, this paper (D. Gordon)	NNZ
Loxosomatid sp. 1	on sipunculan *Phascolosoma*	Whitelegge 1889	NSW
Loxosomatid sp. 2	on hirudinean *Branchellion*	Goddard 1909	WA
Loxosomatid sp. 3	on hirudinean *Pontobdella*	Goddard 1909	WA, NSW
Loxosomatid sp. 4	on bryozoan *Amathia*	Harmer 1915	VIC
Loxosomatid sp. 5	on squat lobster *Thenus*	Wasson, this paper (R. Lester)	QLD
Loxosomatid sp. 6	on aquarium walls	Gordon & Ballantine 1977	NNZ

FAMILY PEDICELLINIDAE (6 described species)

Pedicellina cernua	(Pallas, 1774)	Kirkpatrick 1890b; Chittleborough[1]; Wasson 1995	VIC, SA
Pedicellina compacta	Harmer, 1915	Hastings 1932; Wasson 1995	QLD
Pedicellina grandis	Ryland, 1965	Ryland 1965	SNZ
Pedicellina pernae	Ryland, 1965	Ryland 1965	SNZ
Pedicellina pyriformis	Ryland, 1965	Ryland 1965, Wasson 1995	SNZ, TAS
Pedicellina whiteleggii	Johnston & Walker, 1917	Wasson 1995 (and others cited therein)	NSW, VIC, SA, NNZ, SNZ

FAMILY BARENTSIIDAE (6 described + 1 undescribed species)

Barentsia benedeni	(Foettinger, 1887) [misidentified as *B. gracilis*]	Wasson & Shepherd 1997; Chittleborough[1]	NSW, SA SA
Barentsia discreta	(Busk, 1886)	Wasson & Shepherd 1997 Wasson, this paper (D. Gordon & S. O'Shea)	VIC NNZ
Barentsia geniculata	Harmer, 1915	Wasson, this paper (R. A. Birtles & P. Arnold)	QLD
Barentsia laxa	Kirkpatrick, 1890a	Kirkpatrick 1890a	NT
Barentsia matsushimana	Toriumi, 1951	Wasson, this paper (M. Barker & K. Wasson)	SNZ
Barentsia sp. 1	minute, delicate zooids [misidentified as *B. gracilis*]	Wasson & Shepherd 1997; Kirkpatrick 1890b; Waters 1904; Hastings 1932; Hilgendorf 1898; Gordon 1972	NSW, SNZ, SA VIC, QLD SNZ, NNZ
Pedicellinopsis fruticosa	Hincks, 1884	Hincks 1884; Busk 1886; MacGillivray 1887; Whitelegge 1889; Hedley 1915; Johnston & Angel 1940; Wasson & Shepherd 1997	VIC, NSW, TAS

[1] Chittleborough, R. G. (1952) Marine Fouling at Port Adelaide. MSc Thesis, The University of Adelaide (unpub.).